Stochastic dynamics and mean field approach in a system of three interacting species

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Abstract

The spatio-temporal dynamics of three interacting species, two preys and one predator, in the presence of two different kinds of noise sources is studied. To describe the spatial distributions of the species we use a model based on Lotka-Volterra equations. A correlated dichotomous noise acts on β, the interaction parameter between the two preys, and a multiplicative white noise affects directly the dynamics of each one of the three species. We study the time behaviour of the three species in single site for different values of the multiplicative noise intensity, finding noise-induced oscillations of the three species densities with an anticorrelated behaviour of the two preys. Afterwards, by considering a spatially extended system formed by a two-dimensional lattice with N sites and applying a mean field approach, we get the corresponding moment equations in Gaussian approximation. Within this formalism we obtain the time behaviour of the first and second order moments for different values of multiplicative noise intensity, with $\beta(t)$ subject to the same dichotomous noise source. Finally, we compare our results with those obtained by using a coupled map lattice model, consisting of a time discrete version of the Lotka-Volterra equations.

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I. INTRODUCTION

Noise is not generally detrimental to biological systems but can be employed to generate genotypic, phenotypic, and behavioral diversity [1, 2, 3, 4]. Real ecosystems are affected by the presence of noise sources which consist of random variability of environmental parameters, such as temperature, food availability, general conditions which can favour or thwart the increase of some biological species. This randomly fluctuating behaviour can be modeled by Gaussian noise sources, which influence, through a multiplicative interaction, the system dynamics. Multiplicative noise often causes the appearance of fluctuating barriers or processes of anomalous diffusion and has been investigated in the context of population growth and extinction [1, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15]. In this paper we study the time evolution of three interacting species, two preys, x and y, and one predator, z. The interaction between the two preys is symmetric and it is given by the parameter β. We study the ecosystem dynamics, described by generalized Lotka-Volterra equations, in the presence of two different kinds of noise sources: (i) a dichotomous noise acting on the β parameter, (ii) three external sources, modeled as independent multiplicative Gaussian noises, which act directly on the three species. First we consider the deterministic dynamics of the system in a single site and we get the time behaviour of x, y and z, by analyzing the stability of the ecosystem with different constant values of the interaction parameter β, which correspond to a coexistence regime ($\beta_{down} < 1$) or to an exclusion regime ($\beta_{up} > 1$). Then we consider the interaction parameter β varying dichotomously between these two values. In this condition we study the time behaviour of the species concentrations x, y and z for different levels of the multiplicative noise intensity. We find noise-induced oscillations and strong anticorrelations between the preys. Afterwards we take into account the spatial version of our ecosystem, considering a two-dimensional domain formed by N sites and adding a diffusion term in the L-V equations. By using a mean field approach, we obtain the corresponding moment equations in Gaussian approximation. We find that, for β varying dichotomously, the 1st order moments of the three species concentrations are independent on the multiplicative noise intensity. On the other hand, the behavior of the 2nd order moments is strongly affected by the presence of external noise sources. In particular we find that the time behavior is anticorrelated for the species densities of the two preys, and correlated between the predator and the total density of the two preys. Finally we get the time behavior of the 1st and 2nd

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order moments using a coupled map lattice (CML) model [16] and we compare these results with those previously obtained within the mean field approach. In view of an application on real systems, the results obtained could be useful to explain experimental data, reproducing the behaviour of natural ecosystems [5, 6, 17, 18].

II. THE MODEL

Our system is described by a time evolution model of Lotka-Volterra equations, within the Ito scheme, with diffusive terms in a spatial lattice consisting of N sites

$$\dot{x}_{i,j} = \lambda x_{i,j} \left(1 - \nu x_{i,j} - \beta y_{i,j} - \alpha z_{i,j}\right) + x_{i,j} \sqrt{\sigma_x}\, \xi_{i,j}^x + D(<x> - x_{i,j}) \tag{1}$$

$$\dot{y}_{i,j} = \lambda y_{i,j} \left(1 - \nu y_{i,j} - \beta x_{i,j} - \alpha z_{i,j}\right) + y_{i,j} \sqrt{\sigma_y}\, \xi_{i,j}^y + D(<y> - y_{i,j}) \tag{2}$$

$$\dot{z}_{i,j} = \lambda_z z_{i,j} \left[-1 + \gamma \left(x_{i,j} + y_{i,j}\right)\right] + z_{i,j} \sqrt{\sigma_z}\, \xi_{i,j}^z + D(<z> - z_{i,j}), \tag{3}$$

where the dot indicates the time derivative. The variables $x_{i,j}$, $y_{i,j}$ and $z_{i,j}$ are functions of the time t, and denote the densities, respectively, of the two preys and the predator in the lattice site (i, j). λ and λ_z are scale factors, ν is the growth rate for the two preys, D is the diffusion coefficient, and $<x>$, $<y>$, $<z>$ indicate the spatial mean, performed on the whole lattice, of the three species densities. The coefficient β is the interaction parameter between the two preys. The coefficients α and γ account for the interaction between preys and predator. $\xi_{i,j}^x(t)$, $\xi_{i,j}^y(t)$, $\xi_{i,j}^z(t)$ are statistically independent Gaussian white noises with zero mean and unit variance, and they model the interaction between species and environment. Finally, σ_x, σ_y, σ_z are the intensities of the three sources of Gaussian white noise.

A. Single site dynamics

1. Stability analysis and dynamical regimes

Depending on the value of the interaction parameter, coexistence or exclusion regimes take place. In the absence both of multiplicative noise ($\sigma_x = \sigma_y = \sigma_z = 0$) and diffusion terms ($D = 0$), Eqs. (1)-(3) describe the deterministic dynamics of a single site ecosystem. In these conditions, for the generic site of lattice the stationary values of the three species

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densities are given by

$$x^{stat} = y^{stat} = \frac{1}{2\gamma} \tag{4}$$

$$z^{stat} = \frac{2\gamma - (\beta + \nu)}{2\alpha\gamma}. \tag{5}$$

where the indices i, j where suppressed. From Eqs. (1)-(3) one can see that the two prey densities have stationary values that are independent on the interaction parameter β. Conversely, the stationary value of the predator density is connected with the value of β. This indicates that the interaction parameter between the two preys determines the coexistence or exclusion regimes for the whole system, affecting the stationary value z^{stat}. From Eq. (5) the survivance condition for the predator is $z^{stat} > 0$, which allows to get the coexistence condition for the three species as a function of β

$$\beta < 2\gamma - \nu. \tag{6}$$

The inequality (6) indicates that the system is characterized by two stationary states, which become stable or unstable depending on the values that β, γ and ν take on. In particular, when the condition (6) is satisfied, the stable state is represented by the coexistence of the three species. Otherwise, after a transient, the predator tends to disappear (inequality (6) doesn't hold anymore) and we get a system formed by two competing species, whose coexistence/exclusion conditions depend directly on the value of the parameter β [17, 19, 20, 21, 22]. In this sense, the predator plays a regulatory role for the dynamics of the two preys, whose reciprocal behavior is mediated by the interaction parameter β through the presence of the species z. We calculate the numerical solutions for single site dynamics, setting in Eqs. (1) - (3) $\lambda = 3$, $\lambda_z = 0.06$, $\nu = 1$, $\alpha = 0.02$, $\gamma = 1$, with two different values $\beta_{down} = 0.94$ and $\beta_{up} = 1.04$ of the interaction parameter β and initial conditions $x(0) = y(0) = 0.1$, $z(0)$ = 2.0. The values of multiplicative noise intensity are the same for the three species, that is $\sigma = \sigma_x = \sigma_y = \sigma_z$. In Fig. 1 we show the time series of the three species in coexistence ($\beta = \beta_{down}$) and exclusion ($\beta = \beta_{up}$) regimes, for $\sigma = 0$ and $\sigma = 10^{-16}$. We note that, when the system is subject to deterministic dynamics, the coexistence regime causes, after a transient, the three species to reach the equilibrium values, $x^{stat} = y^{stat} = 0.5$, $z^{stat} = 1.5$, obtained from Eqs. (4) - (5) using $\nu = 1$, $\alpha = 0.02$, $\gamma = 1$, $\beta = \beta_{down} = 0.94$ (see Fig. 1a). In deterministic exclusion regime the predator tends very slowly to vanish. However, the two prey densities reach the stationary values, remaining constant (Fig. 1b). In this case, the
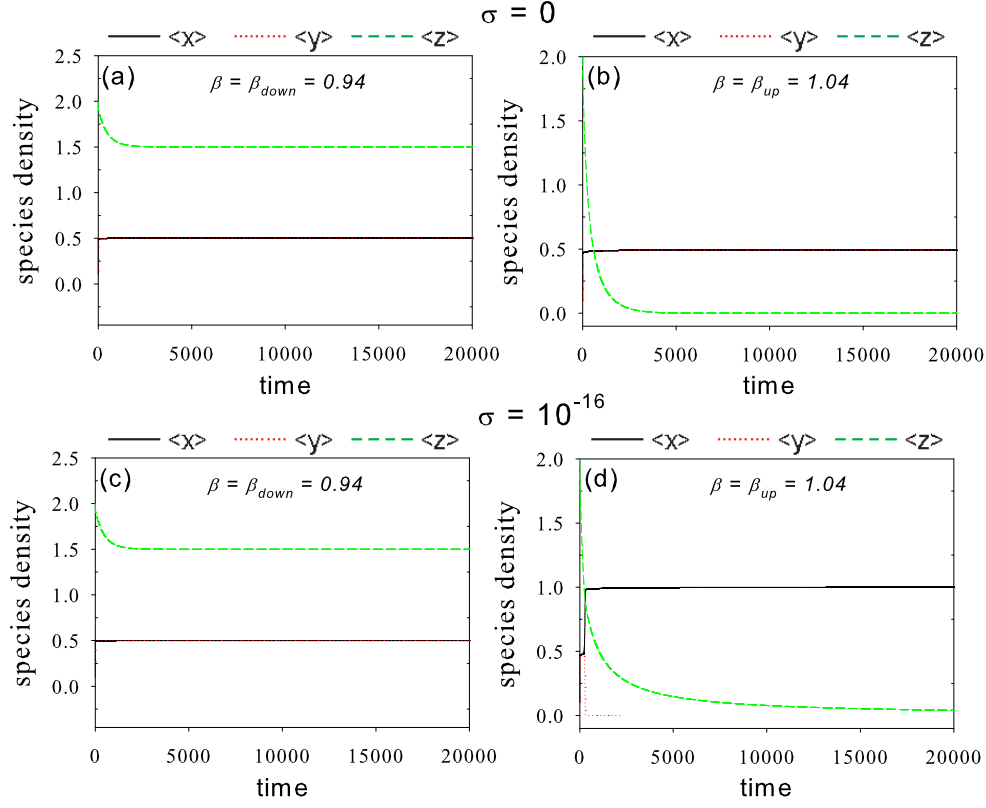
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FIG. 1: Time evolution of the three species. Deterministic dynamics in (a) coexistence and (b) exclusion regime. Stochastic dynamics, for $\sigma = 10^{-16}$ in (c) coexistence and (d) exclusion regime. Values of the parameters and initial conditions are $\lambda = 3$, $\lambda_z = 0.06$, $\nu = 1$, $\alpha = 0.02$, $\gamma = 1$, $x(0) = y(0) = 0.1$, $z(0) = 2.0$.

stationary values correspond to an unstable equilibrium point. In fact, in the presence of a small level of multiplicative noise, the symmetry, due to the parameter values and initial conditions used in our simulations, is broken and one of the two preys prevails, displacing the other one (Fig. 1d), according to the previously obtained results [21]. Finally we note that no significative modifications occur, with respect to the deterministic case, when a small level of noise is present in coexistence regime (see Fig. 1c). This obviously depends on the fact that, for $\beta = \beta_{down}$, the system occupies a stable equilibrium point, which is maintained also in the presence of low levels of multiplicative noise. However, environmental perturbations, due to the presence both of deterministic and random fluctuations of biological and physical variables, such as the temperature, affect the dynamics of the species. These external forces can modify the behaviour of the populations, either introducing multiplicative noise sources
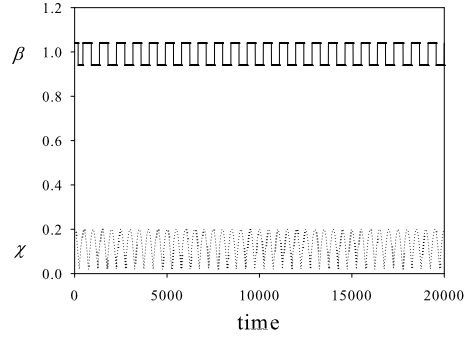
FIG. 2: Time evolution of the interaction parameter $\beta(t)$ with initial value $\beta(0) = 1.04$ and delay time $\tau_d = 435$. The interaction parameter $\beta(t)$ switches quasi-periodically between $\beta_{down} = 0.94$ and $\beta_{up} = 1.04$. The values of the other parameters are $A = 9.0$, $\omega/(2\pi) = 10^{-3}$, $\chi_0 = 2 \cdot 10^{-2}$.

which act directly on the species or affecting the dynamics of the interaction parameter β. In fact, the environmental variations can cause the system dynamics to change between coexistence ($\beta < 2\gamma - \nu$) and exclusion ($\beta > 2\gamma - \nu$) regimes. This dynamical behavior can be described by considering that the interaction parameter $\beta(t)$ is a stochastic process driven by a dichotomous noise, whose jump rate is given by

$$\chi(t) = \begin{cases} 0, & \Delta t \leq \tau_d \\ \chi_0 \left(1 + A \left| \cos \omega t \right|\right), & \Delta t > \tau_d . \end{cases} \tag{7}$$

where Δt is the time interval between two consecutive switches, and τ_d is the delay between two jumps, that is the time interval after a switch, before another jump can occur. In Eq. (7), A and $\omega = (2\pi)/T$ are respectively amplitude and angular frequency of the periodic term, and χ_0 is the jump rate in the absence of periodic term. This causes $\beta(t)$ to jump between two values, $\beta_{down} < 2\gamma - \nu$ and $\beta_{up} > 2\gamma - \nu$. According to the condition (6), these values determine the two possible dynamical regimes (coexistence or exclusion) of the deterministic Lotka-Volterra's model for three interacting species. For given values of the parameters A, ω and χ_0 the switching time between the two levels of $\beta(t)$ depends on τ_d. Applying a procedure analogous to that followed for the two-species case [19], we set $A = 9.0$, $\omega/(2\pi) = 10^{-3}$, $\chi_0 = 2 \cdot 10^{-2}$, obtaining the time series of $\beta(t)$ for $\tau_d = 435$, with $\beta_{down} = 0.94$ and $\beta_{up} = 1.04$. The results, shown in Fig. 2, indicate the presence of a synchronization between the jumps and the periodicity of the rate $\chi(t)$. For a system formed by two competing species this causes a quasi-periodical time behavior of the two populations, which

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can be considered as a signature of the stochastic resonance phenomenon [24] in population dynamics [20, 21, 22]. Therefore we fix the delay at the value $\tau_D = 435$, which determines an oscillating dynamical regime. In these conditions, $\beta(t)$ switches quasi-periodically between β_{down} and β_{up} (see Fig. 2), causing the system to be alternatively subject to the coexistence and exclusion regimes.

2. Time behaviour of the species in a single site

In this section we analyze the time behaviour of three interacting species in a single site of the lattice. From Eqs. (1)-(3), by setting $D = 0$ we get

$$\dot{x} = \lambda x \left(1 - \nu x - \beta y - \alpha z\right) + x \sqrt{\sigma_x} \, \xi^x(t) \tag{8}$$

$$\dot{y} = \lambda y \left(1 - \nu y - \beta x - \alpha z\right) + y \sqrt{\sigma_y} \, \xi^y(t) \tag{9}$$

$$\dot{z} = \lambda_z z \left(-1 + \gamma x + \gamma y\right) + z \sqrt{\sigma_z} \, \xi^z(t), \tag{10}$$

where the indices i, j where suppressed.

By choosing $\beta(0) = 1.04$ and $\tau_d = 435$, we obtain for $\beta(t)$ the time behaviour shown in Fig. 2. We analyze the time evolution of the species densities by numerical simulation of Eqs. (8)-(10). The time series of x, y and z are obtained for different values of the multiplicative noise intensity, namely $\sigma = 0$, 10^{-12}, 10^{-6}, 10^{-3}. The values of the other parameters are the same used in the previous section, that is $\lambda = 3$, $\lambda_z = 0.06$, $\nu = 1$, $\alpha = 0.02$, $\gamma = 1$, $\beta_{down} = 0.94$, $\beta_{up} = 1.04$. The initial values of the species densities are $x(0) = y(0) = 0.1$, $z(0) = 2.0$. In Fig. 3, where the results are reported, the time series of $x(t)$, $y(t)$ (preys) and $z(t)$ (predator) show correlated behaviour in the absence of noise (panel a). In the presence of noise intensity an anticorrelated oscillating behaviour of $x(t)$ and $y(t)$ appears (see panels (b)-(d)). Moreover we note that, for all the values of multiplicative noise intensity, the two prey densities oscillate, with the frequency of the external driving force, around the stationary values, $x^{stat} = y^{stat} = 0.5$. We observe that the predator density show an oscillating behaviour, with the same frequency, around a value smaller than $z^{stat} = 1.5$. However, the oscillations of $z(t)$ are characterized by a larger amplitude with respect to $< x(t) >$ and $< y(t) >$. This behaviour is connected with the different effect that the alternating regime (exclusion/coexistence) produces on preys and predator. In fact, the quasi-periodical behaviour of $\beta(t)$ affects directly the dynamics of the predator (see
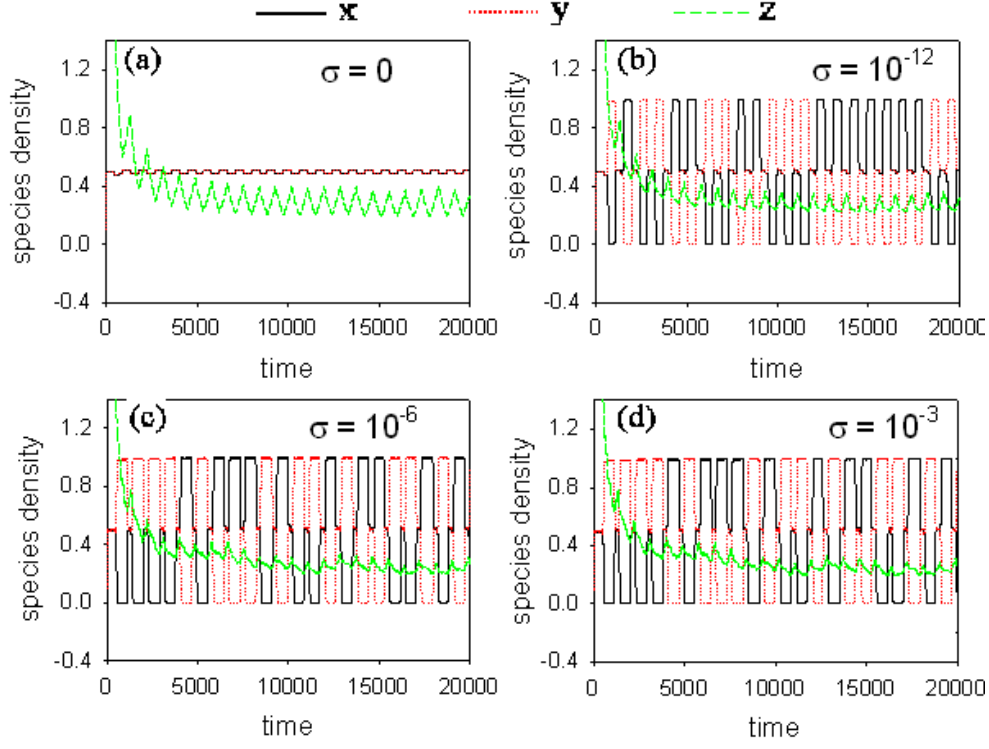
FIG. 3: Time evolution of the three species densities in a single site of the lattice. The values of the multiplicative noise intensity are: (a) $\sigma = 0$, (b) $\sigma = 10^{-12}$, (c) $\sigma = 10^{-6}$, (d) $\sigma = 10^{-3}$. Here $\lambda = 3$, $\lambda_z = 0.06$, $\nu = 1$, $\alpha = 0.02$, $\gamma = 1$. The values of the other parameters are the same of Fig. 2. The initial values of the species densities are $x(0) = y(0) = 0.1$, $z(0) = 2.0$. The time series of $x(t)$, $y(t)$ (preys) and $z(t)$ (predator) show a correlated behaviour in the absence of noise (panel a). In the presence of the noise (panels (b)-(d)) an anticorrelated behaviour of $x(t)$ and $y(t)$ appears.

Eq. 5), causing a decrease of the mean value of z during the exclusion regime. Conversely, in coexistence regime the two preys maintain a constant value (see Eq. (4)) going towards an anticorrelated regime for $\beta(t) = \beta_{up}$. In this last condition the two preys are subject to a pure competitive dynamics, recovering the behaviour observed in a system of two competing species [21].

B. Spatially extended system: Mean field approach

In this section we analyze the time behaviour of three interacting species in a spatially extended system by using a mean field approach. The system dynamics is described by Eqs. (1)-(3) in the presence of the diffusive term ($D \neq 0$). In order to use a mean field approach we derive the moment equations for this system. Assuming $N \to \infty$, we write Eqs. (1)-(3) in a mean field form

$$\dot{x} = f_x(x,y,z) + \sqrt{\sigma_x}\, g_x(x)\, \xi^x(t) + D(<x> -x), \tag{11}$$

$$\dot{y} = f_y(x,y,z) + \sqrt{\sigma_y}\, g_y(y)\, \xi^y(t) + D(<y> -y), \tag{12}$$

$$\dot{z} = f_z(x,y,z) + \sqrt{\sigma_y}\, g_z(y)\, \xi^z(t) + D(<z> -z), \tag{13}$$

where $<x>$, $<y>$ and $<z>$ are average values on the spatial lattice considered (ensemble averages in the thermodynamic limit) and we set $f_x(x,y,z) = \lambda x(1-\nu x-\beta y-\alpha z)$, $g_x(x) = x$, $f_y(x,y,z) = \lambda y(1 - \nu y - \beta x - \alpha z)$, $g_y(y) = y$, $f_z(x,y,z) = \lambda_z z[-1 + \gamma(x + y)]$, $g_z(z) = z$. By site averaging Eqs. (11)-(13), we obtain

$$<\dot{x}> \;=\; <f_x(x,y,z)>, \quad <\dot{y}> \;=\; <f_y(x,y,z)>, \quad <\dot{z}> \;=\; <f_z(x,y,z)> . \tag{14}$$

By expanding the functions $f_x(x,y,z)$, $g_x(x)$, $f_y(x,y,z)$, $g_y(y)$, $f_z(x,y,z)$, $g_z(z)$ around the 1st order moments $<x(t)>$, $<y(t)>$ and $<z(t)>$, we get an infinite set of simultaneous ordinary differential equations for all the moments [25]. To truncate this set we apply a Gaussian approximation, for which the cumulants above the 2nd order vanish. Therefore we

obtain

$$< \dot{x} > \ = \ \lambda < x > (1 - \nu < x > -\beta < y > -\alpha < z >) - \lambda(\nu \mu_{200} + \beta \mu_{110} + \alpha \mu_{101}) \quad (15)$$

$$< \dot{y} > \ = \ \lambda < y > (1 - \nu < y > -\beta < x > -\alpha < z >) - \lambda(\nu \mu_{020} + \beta \mu_{110} + \alpha \mu_{011}) \quad (16)$$

$$< \dot{z} > \ = \ \lambda_z < z > (-1 + \gamma < x > +\gamma < y >) + \lambda_z \gamma(\mu_{101} + \mu_{011}) \quad (17)$$

$$\dot{\mu}_{200} \ = \ 2\lambda(1 - 2\nu < x > -\beta < y > -\alpha < z >)\mu_{200}$$
$$- \ 2\lambda < x > (\beta \mu_{110} + \alpha \mu_{101}) + 2\sigma_x(\mu_{200} + < x >^2) - 2D\mu_{200} \quad (18)$$

$$\dot{\mu}_{020} \ = \ 2\lambda(1 - 2\nu < y > -\beta < x > -\alpha < z >)\mu_{020}$$
$$- \ 2\lambda < y > (\beta \mu_{110} + \alpha \mu_{011}) + 2\sigma_y(\mu_{020} + < y >^2) - 2D\mu_{020} \quad (19)$$

$$\dot{\mu}_{002} \ = \ 2\lambda_z(-1 + \gamma < x > +\gamma < y >)\mu_{002}$$
$$+ \ 2\lambda_z \gamma < z > (\mu_{101} + \mu_{011}) + 2\sigma_z(\mu_{002} + < z >^2) - 2D\mu_{002} \quad (20)$$

$$\dot{\mu}_{110} \ = \ \lambda[2 - 2\nu(< x > + < y >) - \beta(< x > + < y >) - 2\alpha < z >]\mu_{110}$$
$$- \ \lambda\beta(< x > \mu_{020} + < y > \mu_{200}) - \lambda\alpha(< x > \mu_{011} + < y > \mu_{101}) - 2D\mu_{110} \quad (21)$$

$$\dot{\mu}_{101} \ = \ \lambda(1 - 2\nu < x > -\beta < y > -\alpha < z >)\mu_{101} + \lambda_z(-1 + \gamma < x > +\gamma < y >)\mu_{101}$$
$$- \ \lambda < x > (\alpha \mu_{002} + \beta \mu_{011}) + \lambda_z \gamma < z > (\mu_{110} + \mu_{200}) - 2D\mu_{101} \quad (22)$$

$$\dot{\mu}_{011} \ = \ \lambda(1 - 2\nu < y > -\beta < x > -\alpha < z >)\mu_{011} + \lambda_z(-1 + \gamma < x > +\gamma < y >)\mu_{011}$$
$$- \ \lambda < y > (\alpha \mu_{002} + \beta \mu_{101}) + \lambda_z \gamma < z > (\mu_{110} + \mu_{020}) - 2D\mu_{011}. \quad (23)$$

where μ_{200}, μ_{020}, μ_{002}, μ_{110}, μ_{101}, μ_{011} are the 2nd order central moments defined on the lattice

$$\mu_{200}(t) \ = \ < x^2 > - < x >^2, \qquad \mu_{020}(t) \ = \ < y^2 > - < y >^2, \qquad \mu_{002}(t) \ = \ < z^2 > - < z >^2,$$

$$\mu_{110}(t) \ = \ < xy > - < x >< y >, \quad \mu_{101}(t) \ = \ < xz > - < x >< z >, \quad \mu_{011}(t) \ = \ < yz > - < y >< z$$

In order to get the dynamics of the three species we analyze the time evolution of the 1st and 2nd order moments according to Eqs. (15)-(23). As initial conditions we consider each species uniformly distributed on the spatial domain, that is we set $< x(0) > \ = \ < y(0) > \ = \ 0.1$, $< z(0) > \ = \ 2.0$, $\mu_{200}(0) \ = \ \mu_{020}(0) \ = \ \mu_{002}(0) \ = \ \mu_{110}(0) \ = \ \mu_{101}(0) \ = \ \mu_{011}(0) \ = \ 0$. Therefore, from Eqs. (15)-(23) we get, in the deterministic case, the stationary values for $< x >$, $< y >$ and $< z >$

$$< x >^{stat} \ = \ < y >^{stat} \ = \ \frac{1}{2\gamma}, \quad < z >^{stat} \ = \ \frac{2\gamma - (\beta_{down} + \nu)}{2\alpha\gamma}. \quad (25)$$

Using for the parameters the same values of the single site analysis, we obtain $< x >^{stat} = < y >^{stat} = 0.5$ and $< z >^{stat} = 1.5$. We also fix the delay time at the same value $\tau_d = 435$ used in the single site case. Finally, by numerical integration of Eqs. (15)-(23), setting $D = 10^{-1}$, we get the time series of the 1st and 2nd order moments for the following values of multiplicative noise intensity $\sigma = 0, 10^{-12}, 10^{-6}, 10^{-3}$. The results are reported in Figs. 4, 5. Here we note that, after a transient, the mean values of the two prey densities (see panels a and d of Figs. 4, 5) oscillate around the stationary values. The oscillations are connected with the presence of two stable equilibrium points. For $\beta = \beta_{down} < 1$ the stable equilibrium is given by the contemporary presence of the three species (coexistence regime). Conversely, for $\beta = \beta_{up} > 1$ the system goes towards a new equilibrium point, with the predator tending to disappear (exclusion regime). In the presence of a dynamical regime (the system switches periodically from coexistence to exclusion), we observe the appearance of correlated oscillations in the time series of $< x(t) >$, $< y(t) >$ and $< z(t) >$. In particular, we note that $< z(t) >$ is subject to oscillations occurring around a value smaller than the stationary one ($< z >^{stat} = 1.5$) and characterized by a larger amplitude with respect to $< x(t) >$ and $< y(t) >$. This behaviour is analogous to that observed in the case of single site dynamics. In the absence of noise (top of Fig. 4), the time series of $< x(t) >$, $< y(t) >$ and $< z(t) >$ (panel a), $\mu_{200}(t)$, $\mu_{020}(t)$, $\mu_{002}(t)$ (panel b) and $\mu_{110}(t)$, $\mu_{101}(t)$, $\mu_{011}(t)$ (panel c) are completely overlapped and each species maintains a homogeneous distribution over the lattice, that is all the 2nd order moments remain equal to zero. For $\sigma = 10^{-12}$ (bottom of Fig. 4) no changes are observed in the behaviour of the mean values (see panel d), and the variances of the three species show correlated oscillations (panel e). In panel f, μ_{110} oscillates taking on only negative values. This indicates that the spatial distributions in the lattice will be characterized by the presence of regions where species x or species y prevails. The two preys will be distributed therefore in non-overlapping spatial patterns. This picture is in agreement with previous results obtained with a different model [23]. Conversely, μ_{101} and μ_{011} are always zero (see panel f of Fig. 4). This behaviour indicates that the predator is uncorrelated with the density of each prey: the species z tends to occupy indifferently the sites where x or y prevails (see the time behaviour of μ_{002} in panel e of Fig. 4), but is correlated with the total prey density (a global increase of food availability improves the life conditions of the predator). This explains why the variance of the predator shows small oscillations. On the other hand, when exclusion regime takes place, the two preys tend to
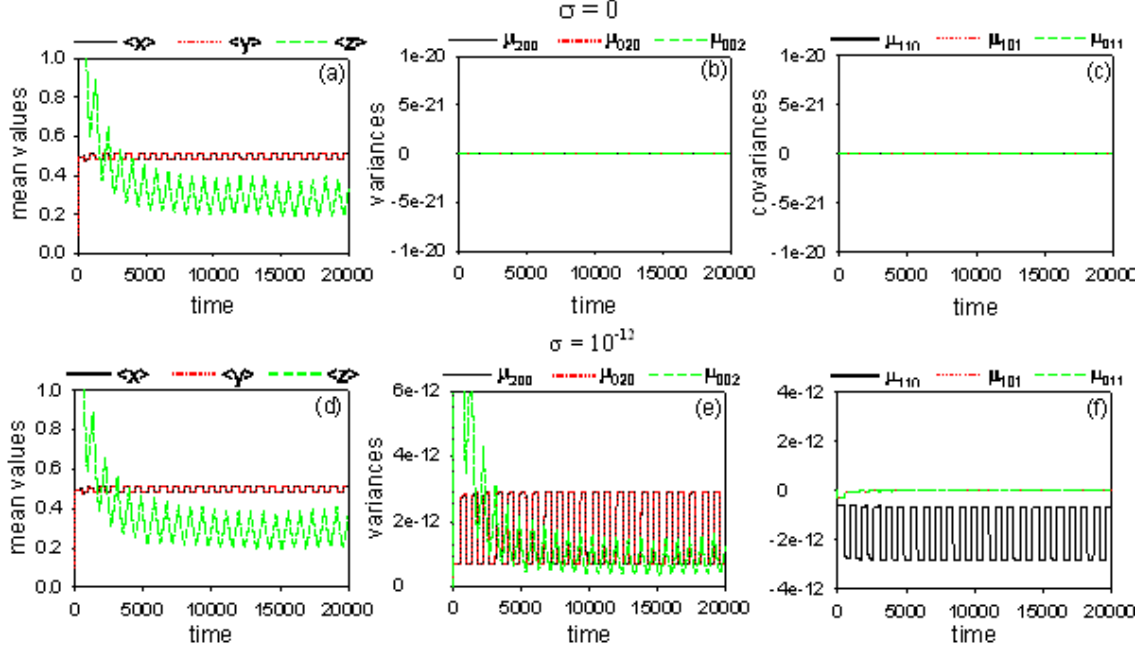
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FIG. 4: Time evolution of the 1st and 2nd order moments in the mean field approach. The values of the multiplicative noise intensity are: $\sigma = 0$, 10^{-12} from top to bottom. In the absence of noise the time series of $< x(t) >$, $< y(t) >$ (panel a), μ_{200}, μ_{020}, μ_{002} (panel b) and μ_{110}, μ_{101}, μ_{011} (panel c) are completely overlapped. The predator (mean value of species z) shows a behaviour correlated with those of both preys (mean values of species x and y). For $\sigma = 10^{-12}$, no changes are observed in the behaviour of the mean values (panel d), the variances of the two preys oscillate overlapping each other and a correlation is observed with the variance of the species z (panel e), the covariance of the two preys, μ_{110}, oscillates taking on only negative values (the two preys are anticorrelated each other), while μ_{101} and μ_{011} are always zero (panel f). The initial values of the moments are $< x(0) > = < y(0) > = 0.1$, $< z(0) > = 2.0$, $\mu_{200}(0) = \mu_{020}(0) = \mu_{002}(0) = \mu_{110}(0) = \mu_{110}(0) = 0 = \mu_{011}(0) = 0$. The diffusion coefficient is $D = 10^{-1}$. The values of the other parameters are the same used in Fig. 3.

occupy different sites, "spreading out" in the spatial domain and causing an increase of their variances (see panel e of Fig. 4) with a stronger anticorrelation (see the behaviour of μ_{110} in panel f of Fig. 4). Finally we note that the amplitude of the oscillations both of the variances and covariances increases as a function of the noise intensity: in particular they have the same order of magnitude of σ (see panels b, c, e, f, in Figs. 4, 5). In fact, for higher
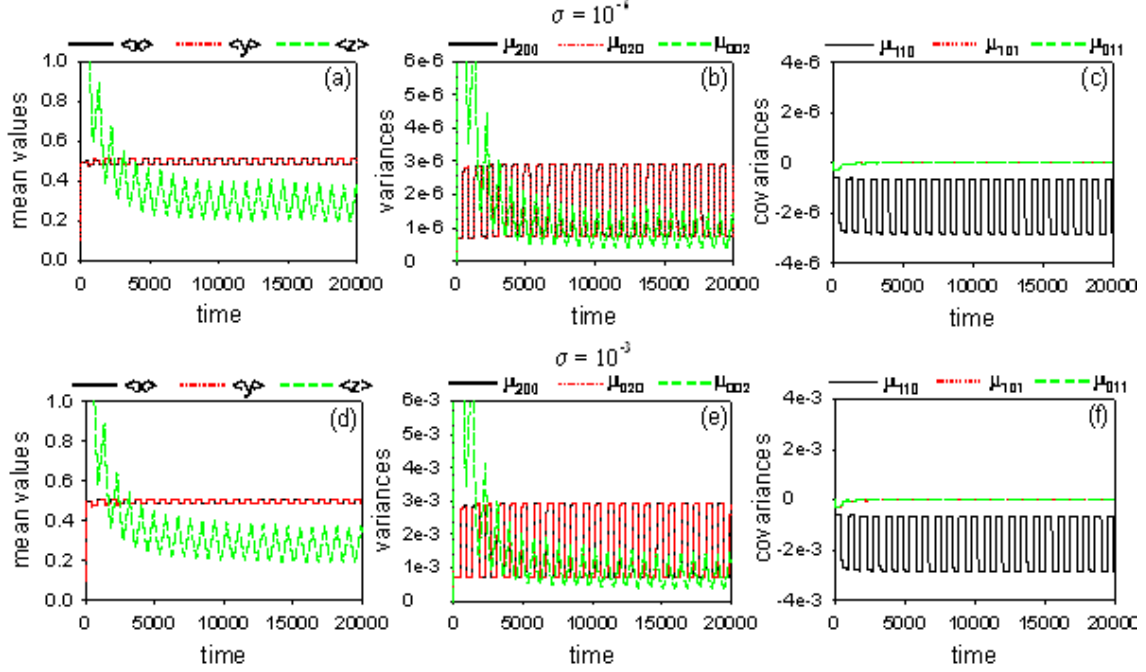
FIG. 5: Time evolution of the 1st and 2nd order moments. The values of the multiplicative noise intensity are: 10^{-6}, 10^{-3} from top to bottom. No changes are observed in the time behaviour of $< x > = < y > = < z >$ (see panels a and d) for both values of the noise intensity. An increase in the amplitude of oscillations, as a function of the noise intensity, appears both in the variances of the two predators, μ_{200}, μ_{020}, (see panels b and e) and in the covariance of the two preys, μ_{110}, (see panels c and f). The values both of initial conditions and parameters are the same used in Fig. 5.

levels of multiplicative noise ($\sigma = 10^{-6}, 10^{-3}$) the amplitude of the oscillations increases and the periodical anticorrelated behaviour between the two preys becomes more evident. Conversely, no modifications appear in the time series of the mean values as a function of the multiplicative noise intensity (see panels a, d in Figs. 4, 5).

Even if it is related to a very different mechanism, this behavior is similar to the stochastic resonance effect produced in population dynamics, when the interaction parameter is subjected to an oscillating bistable potential in the presence of additive noise [21, 22]. We note that in the absence of external noise ($\sigma = 0$) both populations coexist and the species densities oscillate in phase around their stationary value [21]. This occurs identically in each site of the spatial lattice (single site dynamics). The behavior of the mean values reproduces this situation. For $\sigma \neq 0$, in the single site dynamics we observe anticorrelated oscillations of

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x and y (preys). By site averaging these noise-induced oscillations (see Ref. [21]) we recover the average behavior obtained in the absence of noise. This spatial auto-averaging effect explains why the 1st order moment behavior is independent on the external noise intensity, while the 2nd order moments give information on "spreading" and anticorrelation of the species densities in the spatial domain.

III.   COUPLED MAP LATTICE MODEL

In this section we adopt a different approach to analyze the dynamics of the three species on the square lattice defined in Section II. We consider the time evolution of our system by using a coupled map lattice (CML) model [16]. In this formalism both correlated and anticorrelated spatial patterns of the three interacting species have been found [23]. Here we calculate the moments by using the CML model. By this approach, the dynamics of the spatial distributions of the three species is given by the following equations

$$x_{i,j}^{(n+1)} = \lambda x_{i,j}^{(n)}(1 - \nu x_{i,j}^{(n)} - \beta^{(n)} y_{i,j}^{(n)} - \alpha\, z_{i,j}^{(n)}) + \sqrt{\sigma_x} x_{i,j}^{(n)} \xi_{i,j}^{x(n)} + D \sum_{\rho}(x_{\rho}^{(n)} - x_{i,j}^{(n)}), \quad (26)$$

$$y_{i,j}^{(n+1)} = \lambda y_{i,j}^{(n)}(1 - \nu y_{i,j}^{(n)} - \beta^{(n)} x_{i,j}^{(n)} - \alpha\, z_{i,j}^{(n)}) + \sqrt{\sigma_y} y_{i,j}^{(n)} \xi_{i,j}^{y(n)} + D \sum_{\rho}(y_{\rho}^{(n)} - y_{i,j}^{(n)}), \quad (27)$$

$$z_{i,j}^{(n+1)} = \lambda_z z_{i,j}^{(n)}(-1 + \gamma\, x_{i,j}^{(n)} + \gamma\, y_{i,j}^{(n)}) + \sqrt{\sigma_z} z_{i,j}^{(n)} \xi_{i,j}^{z(n)} + D \sum_{\rho}(z_{\rho}^{(n)} - z_{i,j}^{(n)}), \quad (28)$$

where $x_{i,j}^{(n)}$, $y_{i,j}^{(n)}$ and $z_{i,j}^{(n)}$ denote respectively the densities of prey x, prey y and predator z in the site (i,j) at the time step n. According to the notation used for the mean field approach, λ, λ_z, ν, β, α, γ and D represent the same quantities defined in Section II. $\xi_{i,j}^{x(n)}$, $\xi_{i,j}^{y(n)}$, $\xi_{i,j}^{z(n)}$ are independent Gaussian white noise sources with zero mean and unit variance. The interaction parameter $\beta^{(n)}$ corresponds to the value of $\beta(t)$ taken at the time step n, according to Eq. (7). Here $\sum_{\rho}$ indicates the sum over the four nearest neighbours.

A.   Stationary states for the CML model

Applying a procedure analogous to that used for Eqs. (1)-(3), we consider Eqs. (26)-(28) in the absence both of noise sources and diffusion terms ($D = 0$). In this conditions, for $x_{i,j}^{(n+1)} = x_{i,j}^{(n)}$, $y_{i,j}^{(n+1)} = y_{i,j}^{(n)}$, $z_{i,j}^{(n+1)} = z_{i,j}^{(n)}$, we obtain the stationary values of the three species

densities for the generic site

$$x^{stat}_{CML} = y^{stat}_{CML} = \frac{1}{2\gamma}\left[\frac{\lambda_z + 1}{\lambda_z}\right] \tag{29}$$

$$z^{stat}_{CML} = \frac{2\gamma\left[\frac{\lambda-1}{\lambda}\right] - (\beta + \nu)\left[\frac{\lambda_z+1}{\lambda_z}\right]}{2\alpha\gamma}, \tag{30}$$

where the indices i, j were suppressed. As in the approach based on the use of differential equations, the stationary values of the two prey densities are independent on the interaction parameter β, which is responsible for the two different dynamical regimes, coexistence or exclusion, and affects the dynamics of the whole system through its action on the stationary value z^{stat}_{CML}. The existence condition for the predator

$$z^{stat}_{CML} = \frac{2\gamma\left[\frac{\lambda-1}{\lambda}\right] - (\beta + \nu)\left[\frac{\lambda_z+1}{\lambda_z}\right]}{2\alpha\gamma} > 0 \tag{31}$$

allows to get the following inequality for the interaction parameter β

$$\beta < 2\gamma\frac{\left[\frac{\lambda-1}{\lambda}\right]}{\left[\frac{\lambda_z+1}{\lambda_z}\right]} - \nu. \tag{32}$$

The inequality (32) indicates that, according to the analysis performed in Section II A, the CML model is characterized by two stationary states that become stable or unstable depending on the values of the parameters. Comparing the inequalities (6) and (32), we note that in the CML model the coexistence condition and the regulatory role, played by the predator on the dynamics of the two preys, depend also on the scale factors λ and λ_z.

B. Time series in the CML model

In view of a comparison between mean field approach and CML model, we define the 1st and 2nd order moments on the discrete lattice, at the time step n. The mean values, $< x >^{(n)}$, $< y >^{(n)}$, $< z >^{(n)}$, given by

$$< u >^{(n)} = \frac{\sum_{i,j} u^{(n)}_{i,j}}{N} \qquad (u = x, y, z) \tag{33}$$

represent the 1st order moments. The variances $var^{(n)}_x$, $var^{(n)}_y$, $var^{(n)}_z$ defined as

$$var^{(n)}_u = \frac{\sum_{i,j}(u^{(n)}_{i,j} - < u >^{(n)})^2}{N} \qquad (u = x, y, z), \tag{34}$$

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and the covariances

$$cov_{uw}^{(n)} = \frac{\sum_{i,j}(u_{i,j}^{(n)} - <u>^{(n)})(w_{i,j}^{(n)} - <w>^{(n)})}{N} \quad (u, w = x, y, z, \ u \neq w) \qquad (35)$$

are the 2nd order central moments. In order to get, for the species densities, stationary values close to those obtained in the mean field approach (see Eqs. (25)), we choose for all the parameters, except γ, the same values of Section II. Therefore, setting $\lambda = 3$, $\lambda_z = 0.06$, $\nu = 1$, $\alpha = 0.02$, $\gamma = 26.5$, from Eqs. (29), (30), we calculate the stationary values for the densities of the two preys and predator in the coexistence regime ($\beta = \beta_{down} = 0.94$)

$$<x>_{CML}^{stat} \ = \ <y>_{CML}^{stat} \ = \ 0.3 \ ; \quad <z>_{CML}^{stat} \ = \ 1.0. \qquad (36)$$

The CML model can be considered as a time discrete version of the Lotka-Volterra system, with time step $\Delta t = 1$. For the numerical integration of Eqs. (15)-(23) we used $dt = 10^{-3}$, which is a suitable value to obtain convergence of the solution. Obviously, with these values of Δt and dt, the dynamics of the CML model results to be faster with respect to that obtained within the moment formalism. In particular, for $\beta = \beta_{up} > 1$, using the same parameter values of the mean field approach, the exclusion regime causes the species z to vanish in one time step ($\Delta t = 1$). This implies that, when the system is subject to the dynamical regime discussed in Section II A, the predator disappears. This behaviour disagrees with the results found by using the moment equations (see Section II B). In order to remove this discrepancy between CML model and mean field approach, in the discrete time equations we use a much smaller value for the diffusion constant, namely $D = 10^{-4}$. By this way, we obtain a slowdown of the diffusion dynamics and, as a consequence, the survivance of the predator in the coexistence/exclusion dynamical regime. In order to get the time behaviour of the 1st and 2nd order moments within the scheme of the CML model, we consider a square lattice with $N = 100 \times 100$, using for $\beta(t)$ the time behaviour given in Fig. 2. Afterwards, at each time step n we calculate, from Eqs. (26), (27), (28), the new values of $x_{i,j}^{(n)}$, $y_{i,j}^{(n)}$, $z_{i,j}^{(n)}$, and the moments according to Eqs. (33), (34), (35). By iterating this procedure, we obtain the time series shown in Figs. 6, 7. The 1st and 2nd order moments calculated within the formalism of the CML model can be compared with the same quantities obtained in the mean field approach (see Figs. 4, 5). We note that the two set of time series are in a good qualitative agreement. According to the results obtained in the formalism of the moment equations, the mean values of the three species show time oscillations, whose
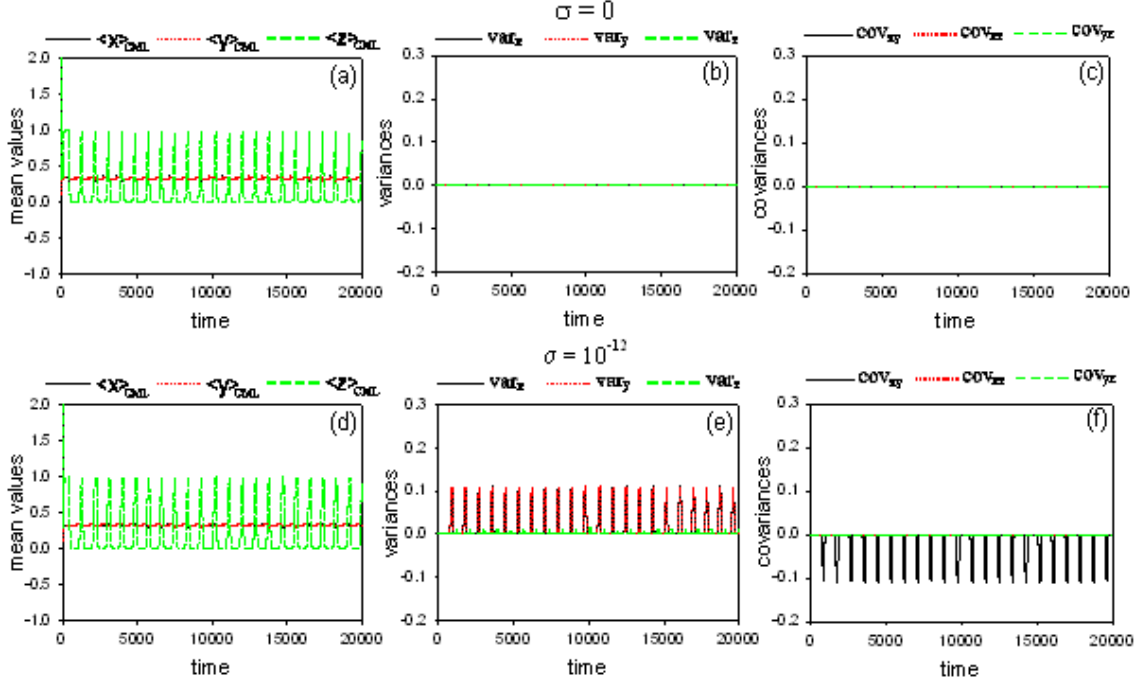
16

FIG. 6: In panels (a), (b) and (c) we show, respectively, the mean values, $< x >^{(n)}$, $< y >^{(n)}$, $< z >^{(n)}$, the variances, $var_x^{(n)}$, $var_y^{(n)}$, $var_z^{(n)}$, and the covariances, $cov_{xy}^{(n)}$, $cov_{xy}^{(n)}$, $cov_{xy}^{(n)}$ for $\sigma = 0$. The same quantities are shown in panels (d), (e) and (f) for $\sigma = 10^{-12}$. The time series are obtained within the formalism of the CML model (see Eqs. (26), (27), (28)). The diffusion coefficient is $D = 10^{-4}$, and $\gamma = 26.5$. The initial values of the species concentrations are $x_{i,j}^{(0)} = y_{i,j}^{(0)} = 0.1$, $z_{i,j}^{(0)} = 2.0$ for all the sites (i,j). The values of the other parameters are the same of Fig. 4: $\lambda = 3$, $\lambda_z = 0.06$, $\nu = 1$, $\alpha = 0.02$.

amplitude is larger for the predator (panels a, d of Figs. 6, 7). In the absence of noise, the 2nd order moments remain equal to zero (see panel b of Fig. 6), recovering the conditions of homogeneous distributions obtained for $\sigma = 0$ in the mean field approach (see panel b of Fig. 4). In the presence of multiplicative noise, no modifications occur in the time series of the 1st order moments (see left side panels in Figs. 6, 7). However, for $\sigma \neq 0$ a symmetry breaking is introduced, with non-vanishing variances that are responsible for inhomogeneous distributions of the three species. For higher levels of the noise intensity, the amplitude of the oscillations remains constant in the time series of var_x, var_y and var_z (see panels b, e of Figs. 6, 7). These results show some difference with those obtained in the formalism of moment equations, where higher noise intensities cause the oscillation amplitudes of μ_{200},
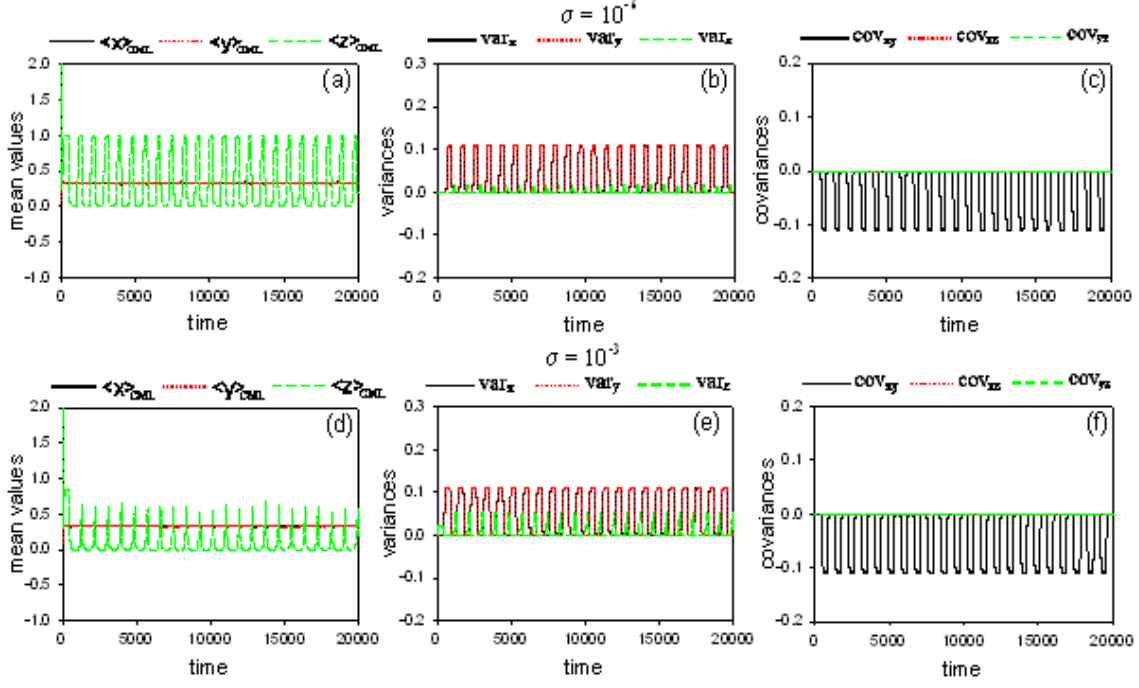
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FIG. 7: In panels (a), (b) and (c) we show, respectively, the mean values, $< x >^{(n)}$, $< y >^{(n)}$, $< z >^{(n)}$, the variances, $var_x^{(n)}$, $var_y^{(n)}$, $var_z^{(n)}$, and the covariances, $cov_{xy}^{(n)}$, $cov_{xy}^{(n)}$, $cov_{xy}^{(n)}$ for $\sigma = 10^{-6}$. The same quantities are shown in panels (d), (e) and (f) for $\sigma = 10^{-3}$. The time series are obtained within the formalism of the CML model (see Eqs. (26), (27), (28)). The values of the other parameters and the initial conditions are the same of Fig. 6.

μ_{020} and μ_{002} to become larger (see panels b, e of Figs. 4, 5). Finally, we find that for $\sigma \neq 0$, temporal oscillations also appear in the time series of μ_{110}. This agrees with the results of the mean field approach, revealing the presence of an anticorrelated dynamics between the two preys. On the other hand, μ_{101} and μ_{011} remain equal to zero also in the presence of multiplicative noise. This behaviour, in agreement with that obtained in the mean field formalism, indicates that the spatial distribution of the predator is uncorrelated with those of each prey considered separately, but depends on the total density of preys. The comparison between the two approaches shows that the mean values $< x >^{(n)}$, $< y >^{(n)}$, $< z >^{(n)}$ and those obtained within the formalism of the moment equations oscillate around different values. Moreover, the amplitudes of the oscillations in the 2nd order moments appear significantly larger in the CML model. This discrepancies can be explained recalling that: i) in the two approaches the stationary values are different (see Eqs. (25) and Eqs. (29)-

(30)); ii) in the mean field formalism the interaction between sites is extended to the whole spatial domain, conversely in the CML model the species interaction is restricted to the nearest neighbors; iii) the dynamics of the CML model is faster since an unitary time step ($\Delta t = 1$) is taken, instead of the time step $dt = 10^{-3}$ used in the moment equations.

IV. CONCLUSIONS

We report a study on the stochastic dynamics of an ecosystem with three interacting species (two preys and one predator), described by generalized Lotka-Volterra equations. After considering the single site dynamics of the ecosystem, we consider a spatially extended domain (two-dimensional lattice) by introducing "long range" diffusive terms (diffusion occurs among each site and all the other ones). The study is performed by a mean field approach, in the formalism of the moment equations. The system is affected by the presence of two noise sources, namely a multiplicative white noise and a correlated dichotomous noise. The role of the correlated dichotomous noise is to control the dynamical regime of the ecosystem (see Fig. 2), while the multiplicative noise is responsible for the anticorrelated behavior of the species concentrations. The mean field approach in Gaussian approximation enables us to obtain the time series of the 1st and 2nd order moments. We compare the results obtained within the mean field approach with the time series calculated by a coupled map lattice (CML) model. The agreement is quite good, even if some discrepancies are present, due to the discrete nature of the CML model and the limited extension of the diffusive interaction (nearest neighbors) among different sites of the coupled map lattice. Our theoretical results could explain the time evolution of populations in real ecosystems whose dynamics is strictly dependent on random fluctuations, always present in natural environment [18, 26, 27].

V. ACKNOWLEDGMENTS

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